

COMMENTS ON *GNAPHALIOTHAMNUS* (ASTERACEAE: INULEAE)

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ABSTRACT

Gnaphaliothamnus is maintained here as a genus of ten species endemic to México and Central America, in contrast to the view of Anderberg (1991) and Freire (1993), who have included most of *Gnaphaliothamnus* within an expanded *Chionolaena* ranging from southern Brazil to northern South America, Central America, and México. Anderberg and Freire restrict *Gnaphaliothamnus* to a single species, which occurs in México and Guatemala, but *Chionolaena seemannii* (Sch.-Bip.) Freire is a synonym of *G. salicifolius*, the generitype of *Gnaphaliothamnus*. A recently described Mexican species, *C. mexicana* Freire, is here regarded as a synonym of *G. concinnus*.

KEY WORDS: *Gnaphaliothamnus*, *Chionolaena*, Gnaphalieae, Inuleae, Asteraceae

In her recently published amalgamation of the genus *Chionolaena* DC., Freire (1993) united species of *Chionolaena*, *Leucopholis* Gardner, *Pseudoligandra* Dillon & Sagást. (Dillon & Sagástegui 1990a), and *Parachionolaena* Dillon & Sagást. (Dillon & Sagástegui 1990b), from South America (southeastern Brazil, Venezuela, and Colombia) with most of the group of Mexican and Central American species earlier treated as *Gnaphaliothamnus* Kirpichn. (Nesom 1990a, 1990b). Freire retained *Gnaphaliothamnus*, however, recognizing it as a monotypic genus (*G. salicifolius* [Bertol.] Nesom, the single species) and as the sister group of *Chionolaena* sensu lato. This restriction of *Gnaphaliothamnus* was first suggested by Anderberg & Freire (1989) and maintained by Anderberg (1991). Freire hypothesized that the Mexican and Central American species are the primitive elements of this whole group (the broadened *Chionolaena* and the monotypic *Gnaphaliothamnus*). Neither my studies (including new species and new combinations within *Gnaphaliothamnus*) nor the second paper published by Dillon & Sagástegui (1990b) have been discussed by Freire or Anderberg.

Freire characterized *Gnaphaliothamnus* (vs. *Chionolaena*) as distinct in its "free pappus bristles" (vs. basally connate) "with linear apical cells" (vs. apical cells of the bristles swollen and the bristles apically clavate). This distinction, however, is not consistent, because the pappus bristles of *G. salicifolius* are often slightly connate at the base, distinctly basally caducous, and released in groups; and while the bristles of *G. salicifolius* are mostly apically attenuate, there is a definite tendency for the apical cells to be swollen and the bristle apex clavate. Further, there is significant interspecific variation within *Gnaphaliothamnus* in these two characters that makes them unreliable as indicators of generic boundaries. Pappus bristles are consistently separate and basally caducous in two species of *Gnaphaliothamnus*: *G. cryptocephalus* Nesom and *G. costaricensis* Nesom; and bristle apices are consistently attenuate at the apex, rather than clavate, in two species: *G. cryptocephalus* and *G. lavandulifolius* (Kunth) Nesom.

An even more interesting indication that a monotypic *Gnaphaliothamnus* cannot be separated from similar Mexican species is the observation that the taxon included by Freire in *Chionolaena* as *C. seemannii* (Sch.-Bip.) Freire is a synonym of *Gnaphaliothamnus salicifolius*, the generic type of *Gnaphaliothamnus*. Freire mapped *C. seemannii* (in her study, this species known only from the type) along the border of the states of Michoacán and Guanajuato, México, based on Seemann's collection "1994" from the "Sierra Madre, NW Mexico." Seemann's route in northwest México, however, began in Mazatlán (Sinaloa), crossed over the Sierra Madre to Ciudad Durango (through southern Durango), ventured south into northeastern Nayarit, and then was retraced back to Ciudad Durango and Mazatlán (Turner 1992). Only two species of *Gnaphaliothamnus* are known from this general area, *G. durangensis* Nesom (rare) and *G. salicifolius* (relatively common). The latter species is easily recognized by its narrow, eglandular, bicolored leaves with essentially glabrous upper surfaces, pedicellate heads in corymbs above the leaves, and large number of pistillate flowers (relative to the central flowers), these features clearly described and illustrated by Freire in *C. seemannii*.

The species most similar and apparently most closely related to *Gnaphaliothamnus salicifolius* is *G. eleagnoides* (Klatt) Nesom. Both species have eglandular, glabrate upper leaf surfaces and a densely corymboid capitulescence of pedicellate heads produced above the leaves. *Gnaphaliothamnus eleagnoides* has somewhat broader leaves, heads with relatively fewer pistillate flowers, and pappus bristles that are distinctly apically clavate, basally persistent, and slightly connate. Possible relationships among the remainder of the species of *Gnaphaliothamnus* are difficult to perceive, but *G. sartorii* (Klatt) Nesom and *G. concinnus* (A. Gray) Nesom also have distinctly short-pedicellate heads and persistently tomentose but eglandular upper leaf surfaces, and these four species may be closely interrelated. The other six species have sessile or nearly sessile heads and glandular leaves (see comments below).

Definition of *Gnaphaliothamnus* vs. *Chionolaena*

Gnaphaliothamnus salicifolius can be absorbed into Freire's broadly conceived *Chionolaena* with no significant phenetic alteration of the latter, but by doing so, the question of the closest relationships of *Chionolaena* sensu Freire and the problem of its internal systematic structure are brought into a different focus. In order to construct a hypothesis of cladistic relationships among the elements of *Chionolaena* in the broadest sense, an outgroup must be sought among other genera. Following Merxmüller *et al.* (1977), Freire noted that *Chionolaena* sensu Freire belongs with the *Lucilia* group, including *Gnaphaliothamnus* sensu stricto and the South American genera *Lucilia* Cass., *Belloa* Remy, *Chevreulia* Cass., *Facelis* Cass., *Cuatrecasasiella* H. Rob., *Mniodes* (A. Gray) Benth., and *Raouliopsis* S.F. Blake.

In Freire's cladistic analysis, however, only *Gnaphaliothamnus* (monotypic) served as the outgroup to her expanded concept of *Chionolaena*, although the same single species of *Gnaphaliothamnus* was included by another name within her circumscription of *Chionolaena*. Using a mix of unweighted characters that appear to vary widely in their potential phyletic significance, Freire's analysis of *Chionolaena* unites some Mexican species with Brazilian ones on the basis of inner involucre bract shape and one Mexican species with the two Colombian ones on the basis of glabrous achene surfaces. There is a perfect correlation, however, between achene pubescence (Freire's character 10) and geography: "villous" achenes occur in the Brazilian taxa and "shortly pubescent" or "glabrous" achenes are found only in the Mexican, Central American, and Colombian taxa.

As I noted earlier (Nesom 1990a), *Gnaphaliothamnus* is distinct from *Chionolaena* in its short achenial hairs with blunt-rounded apices (vs. longer hairs with attenuate-acute apices); such hairs on *G. salicifolius* and *G. lavandulifolius* also were observed to be myxogenic. The achenial hairs of *Gnaphaliothamnus* (sensu Nesom) are relatively homogeneous in morphology and similar to those of the genotype. Anderberg (1991) also characterized the achenial hairs of *G. salicifolius* (= *Gnaphaliothamnus*) as short, clavate, and myxogenic but, apparently following Freire, he provided a general description of the achenial hairs of *Chionolaena* sensu lato (including most of *Gnaphaliothamnus*) as "elongate."

Anderberg's cladistic analysis placed *Gnaphaliothamnus* and *Chionolaena* as sister genera within his "*Anaphalis* group" (of subtribe Cassiniinae Anderberg), a clade that includes *Anaphalis* DC., *Antennaria* Gaertn., *Ewartia* Beauverd, *Anaxeton* Gaertn., *Petalacte* D. Don, and others. The genera of the *Anaphalis* group are spread over South and Central America, South Africa, Asia, North America, Australia, and New Zealand. The remainder of the Cassiniinae, which occupy a coordinate or basal position with respect to the *Anaphalis* group, are restricted to the Australasian area, primarily in Aus-

tralia. Among all these genera, the achenial hairs of *Gnaphaliothamnus* are scored as similar in morphology (character "66. Cypselas hair type") to those of *Antennaria*, *Anaphalis*, and *Ewartia* but not to those of Brazilian *Chionolaena* and *Leucopholis*, although this is not shown on Anderberg's cladograms either as a difference between *Gnaphaliothamnus* and *Chionolaena* or a synapomorphy between *Gnaphaliothamnus* and genera of the *Anaphalis* group. Among the Cassiniinae, the achenial hairs of only *Gnaphaliothamnus*, *Antennaria*, and several Australian genera are known to be myxogenic (Anderberg 1991).

In addition to differences in achenial hairs, Anderberg scored *Chionolaena* and *Gnaphaliothamnus* as different in features of achenial and pappus morphology and sexuality of the central flowers. The degree of basal fusion of pappus bristles (character 79) has already been noted above as variable within *Gnaphaliothamnus*. Anderberg scored the apical cells of pappus bristles (character 80) in *Gnaphaliothamnus* as acute (vs. clavate), but they are characterized as "subclavate" in his description of *Gnaphaliothamnus* as a genus. He scored (incorrectly) the disc flowers of *Gnaphaliothamnus* as fully fertile (character 49), as opposed to sterile in *Chionolaena*. In the morphology of the disc floret achenes (character 58), the achenes of *Gnaphaliothamnus* are scored as "small, oblong" (= the "*Helichrysum* type," a specialization shared with *Antennaria*, *Anaphalis*, and *Ewartia*), while those of *Chionolaena* and all the rest of the Cassiniinae are "ellipsoid or turbinate" (Anderberg 1991). Freire did not make any distinction between achenes, and her illustrations apparently include a mix of mature and immature achenes. Dillon & Sagástegui (1990b) observed that the collecting appendages of the disc flower style branches of *Chionolaena* sensu stricto are lanceolate-acute, in contrast to the rounded or truncate appendages in the other generic-level taxa included by Freire within *Chionolaena*; this difference was not noted by Freire or by Anderberg.

As noted earlier (Nesom 1991) and in the discussion above, the species of *Gnaphaliothamnus* can be divided into two groups on the basis of leaf glandularity. The adaxial leaf surfaces of six species are densely and conspicuously glandular (beneath the dense layer of eglandular tomentum). The glands are "Type C trichomes" (see Nesom 1976; Karis 1993), which also form the characteristic glandularity in much of the Asteroideae. In *Gnaphaliothamnus* they are relatively long, biseriate hairs with thin walls and with a 2-celled head, the distal cells often crumpled and distorted. In the Cassiniinae, such glandularity occurs only in the group of Australian genera that includes *Cassinia* R. Br., *Izodia* R. Br., and *Ozothamnus* R. Br. (Bremer 1991, character 8), and in *Gnaphaliothamnus*. The presence of this glandularity in *Gnaphaliothamnus* was not noted by Freire (1993) nor was it scored by Anderberg (1991).

In summary, the evidence is unconvincing for treating the ten Mexican species of *Gnaphaliothamnus* as congeneric with the essentially Brazilian *Chionolaena* and *Leucopholis*, although it is likely that they are all correctly placed by Anderberg in the subtribe Cassiniinae. With respect to *Gnaphaliothamnus*,

the analyses of both Anderberg and Freire are internally inconsistent as well as contradictory between themselves. Although the hypothesis of a more broadly monophyletic *Chionolaena* cannot be rejected outright, there is evidence to suggest that *Gnaphaliothamnus* (sensu Nesom) may be more closely related to other genera than to *Chionolaena*. *Gnaphaliothamnus* is justifiably maintained as distinct at least until a more thorough study can be provided in a broader context.

Distribution of *Gnaphaliothamnus eleagnoides*

Gnaphaliothamnus eleagnoides (Klatt) Nesom, *Phytologia* 68:376. 1990. BASIONYM: *Chionolaena eleagnoides* Klatt, *Leopoldina* 23:88. 1887. TYPE: MEXICO. [Hidalgo]: "Pelado," Aug 1841, *F. Liebman* 316 (HOLOTYPE: C; fragment and drawing by Klatt-GH!).

In an earlier study (Nesom 1990a), I noted that the type of *Gnaphaliothamnus eleagnoides* was collected in Oaxaca, assuming that the collection was made from the same area as more numerous, recent collections of that species from southeast of Cd. Oaxaca. As correctly observed by Freire (1993), however, the type locality ("Pelado") is in the state of Hidalgo. Compared to the plants from Oaxaca, those from Hidalgo produce slightly broader leaves with a more persistent vestiture on the upper leaf surfaces, but they are similar in other features. Recognition of *G. eleagnoides* in Hidalgo considerably enlarges the distribution of this species.

Comments on *Gnaphaliothamnus concinnus*

Freire (1993) described a new species within *Chionolaena* based on a collection from México by Pringle (originally identified and distributed as *Gnaphalium lavandulaceum* DC.).

Chionolaena mexicana Freire, *Ann. Missouri Bot. Gard.* 80:427. 1993. TYPE: MEXICO. Hidalgo: Sierra de Pachuca, 10,000 ft, 20 Feb 1899, *Pringle* 7700 (HOLOTYPE: K; Isotype: VT!).

I did not examine plants of this collection in my earlier study of the group, but I have now examined a duplicate (VT), which appears to be conspecific with *Gnaphaliothamnus* (*Gnaphalium*) *concinnus* (A. Gray) Nesom. Further, these plants clearly are the same species as identified by Espinosa (1985) as *Gnaphalium concinnum* A. Gray, which I incorrectly referred to as "apparently" *Gnaphaliothamnus salicifolius* (Nesom 1990a). Espinosa cites two other

collections of *G. concinnus* from Hidalgo (north of Pachuca) and one from Edo. México (east of Amecameca).

Freire acknowledged the close relationship between *Chionolaena mexicana* and *C. concinna* (A. Gray) Freire, distinguishing them as follows in her key (1993, p. 408) to the species of *Chionolaena*:

- “16a. Dichotomously branched, rigid shrub; capitulescence terminal at maturity; leaves slightly attenuate at the base. *C. mexicana*
- 16b. Subdichotomously branched subshrub; capitulescence lateral at maturity; leaves subpetiolate. *C. concinna*”

The difference between “dichotomous” and “subdichotomous” branching appears to be variable and subjective; and plants from both areas are erect, otherwise habitally similar, and approximately the same height, even as measured by Freire, so it is not clear why she characterized one as a “shrub” but the other as a “subshrub.” The “lateral” capitulescence of *Chionolaena concinna* may reflect in part the manner in which the plant was originally pressed, with a slight bend near the base of the capitulescence, but the pedicels of the outer heads of *Pringle 7700* tend to be loose with the heads nodding outward (as illustrated by Freire), as is also the case in *C. concinna* sensu stricto. The difference in leaf base is a matter of small degree and application of a similar criterion to other species of *Gnaphaliothamnus* (e.g., *G. salicifolius* and *G. eleagnoides*) would necessitate their taxonomic fragmentation.

I noted earlier (1990a) that the achenial trichomes of *Gnaphaliothamnus concinnus* are narrower than in other species and twisted (this observed from *Schaffner 222-CM*), a feature not observed among the other species. Achenes from other plants of *G. concinnus* in San Luis Potosí, however, appear to have trichomes more similar to those from Hidalgo. The similarity in trichomes of these plants between the two areas also was observed by Freire. More detailed studies of *G. concinnus* may show that some differentiation has occurred among its three general localities (San Luis Potosí, Hidalgo, and Edo. México), the achenes needing particular attention, but there seems to be no clear justification at present for recognizing more than a single species.

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